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Taxa Richness Differences in European Zoos between 1959 and 2016: Establishment Period and the Iron Curtain Matter

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Abstract: Zoos represent a social construct, whose form is influenced by societal development. During the 20th and at the beginning of the 21st century, they have been transformed from assembled collections to internationally managed insurance (ex situ) populations, and these transformations required some changes in taxa numbers and composition. Previous studies have already identified the trend of reducing the number of taxa kept in zoos worldwide. The aim of the present study is to verify this trend in Europe in more detail and therefore to identify the changes in taxa richness and mammalian taxa richness from 1959 to 2016 in the same set of 67 European zoos while considering their opening period (before 1900 and 1900–1960) and location with respect to the former Iron Curtain (Eastern vs. Western Bloc). There was no significant decrease in taxa richness; on the contrary, there was a significant increase in taxa richness for the former Eastern Bloc zoos. There was a significant decrease in mammalian taxa richness for zoos opened before 1900 and those of the former Western Bloc. These results demonstrate that mammalian taxa have declined in numbers to some extent and that the decline mostly concerns older zoos and those that have historically reached a different stage of development. This suggests that European zoos have not been subject to trends uniformly and should apply different and appropriate strategies when facing future (not only conservation) challenges.

Keywords: collection planning; Eastern Bloc; ex situ conservation; mammals; Western Bloc; zoo development

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1. Introduction

Zoos are institutions defined by exhibiting live animals [1]. Modern zoological gardens (hereinafter zoos) should significantly contribute to species conservation through maintaining ex situ populations, public education, research, and initiating, supporting, or funding in situ conservation activities [2]. Their actual form has always reflected various economic, political, environmental, and cultural aspects. In particular, the changes in human-to-animal relations foresaw the evolutionary development of zoos [3], which is also closely linked to the transformation of how humans understand the roles of zoos, with increasing emphasis on nature conservation and animal welfare [4].

Until the 18th century, the so-called menageries represented a symbol of the power and status of nobility and royalty, and the living conditions of the animals were often unsuitable [5,6]. In the 19th century, zoos were designed as taxonomical life museums, focusing on exhibiting as many taxa as possible, with an emphasis on quantity, difference, and otherness [7–10]. Large enclosures for animals would unnecessarily limit exhibiting additional species; thus, the living conditions of the animals were not a priority, and their successful breeding was rather sporadic [11] or accidental [4]. Although many of these zoos established before 1900 did not persist to these days, some of them still exist and belong to one of the most leading European zoos [12]. At the time of their opening, they were located on the outskirts of cities near railway stations [13], and for more than 100 years

of their existence, they have been absorbed by urban development. Consequently, today they struggle with the disadvantage of not having the possibility to expand and increase their area in comparison to zoos established later. Therefore, some zoos established greater facilities outside urban areas as "satellite zoos" beginning in the 1930s (e.g., Whipsnade by the London Zoo) [4].

The further development of European zoos in the 20th century was influenced not only by both World Wars themselves but also by the subsequent political situation. After the Second World War, Europe was divided into Western and Eastern Blocs according to the so-called Iron Curtain, which meant different development of zoos in both regions until 1990, when this Iron Curtain fell.

At the beginning of the postwar period, there were already many zoos in the big cities of the Western Bloc, while there was a very low number of existing zoos in the Eastern Bloc. This difference was related to the diffusion of the industrial revolution and subsequent processes, which came gradually from the west to the east, specifically from the United Kingdom through the Benelux countries to the German-speaking countries. In the second half of the 19th century, this predominantly agricultural region became a highly industrialized and urbanized area. After the Second World War, originally German zoos in Wrocław and Poznań became part of Poland, Eastern Bloc. Also, in the territory of current Czechia, first zoos began to be established in the industrial, then predominantly German-speaking, border regions [14]. In contrast, many other countries of the Eastern Bloc waited for larger industrialization until the 1950s and 1960s, and the first Slovakian zoological gardens did not come into existence until the 1950s. Similarly, in Hungary, there was no zoological garden outside the capital city of Budapest until 1958 [15].

During the Second World War, many Western (and some later Eastern) Bloc zoos were highly damaged [14]. However, they were relatively quickly restored, and in the 1950s, they experienced the highest visitor attendance since their establishment. Nevertheless, this attendance began to decrease sharply soon—due to multiple factors, including the environmental and animal rights movements strongly criticizing the zoos (anti-zoo campaigns) since the 1960s and mainly since the 1970s, respectively [6,16,17]. To prevent their definitive closure, zoos had to accept pivotal and revolutionary steps; key measures were already suggested in the 1940s by Heini Hediger [18], also known as the "father of zoo biology", who emphasized the presentation of the natural behavior of zoo animals. By introducing natural principles, he succeeded in reducing unnatural behavior and increasing animal reproduction and well-being [10]. Additionally, the Washington Convention (CITES), which limited the import of animals from the wild, has been gradually accepted mainly by Western Bloc countries since 1975. Consequently, Western Bloc zoos had to increase the breeding success of their animals and thus significantly improve their living conditions [17].

In comparison to many new Western Bloc zoos established as private or commercial institutions, Eastern Bloc zoos did not have to deal with financial self-sufficiency to such a large extent as they mostly had public ownership. However, they greatly suffered from a lack of extra funds that could be devoted to further development. Due to the division of Europe by the Iron Curtain, they had only limited possibilities for acquiring interesting new species. On the other hand, the Eastern Bloc zoos had privileged access to unique species from the USSR and some extra-European countries belonging to the Communist Bloc (e.g., from Cuba). Newly obtained animals, frequently older individuals, were often housed in temporary exhibits until the 1960s, which was reflected in high mortality and low breeding rates. Larger quantities of individuals suitable for breeding were obtained only from the 1970s, which increased the rate of successful breeding. The animals were mainly sold, which brought in new funds needed for further development, including building new animal houses. In the 1990s, the borders were opened after the fall of the Iron Curtain, which resulted in the connection of animal populations of the Western and Eastern Bloc zoos, with the latter being able to fundamentally change and improve their species collections. Additionally, selling and buying animals was marginalized in the early 1990s

when cooperative breeding programs became incorporated and animals could be acquired free of charge or in exchange [19]. Most Eastern Bloc countries also started to accept the CITES convention after the fall of the Iron Curtain [20].

Generally, during the 20th century, zoos transformed from assembled collections to internationally managed insurance populations [21]. Establishing and maintaining sustainable ex situ populations has required inter-institutional and international cooperation, which has been started since the 1970s and more intensively since the turn of the 1980s and 1990s [22]—on the European level, the European Endangered Species Programmes (EEP; now called EAZA Ex situ Programmes) since 1985 and the European Community Association of Zoos and Aquaria (ECAZA), founded in 1988 and transformed into the European Association of Zoos and Aquaria (EAZA) in 1992 [23]. Local and atypical individuals and common taxa have been replaced (as a part of ex situ conservation) by meaningful taxonomic units and endangered taxa, and single individuals were replaced by appropriate social and breeding groups [7,24,25]. The image of zoos has changed to a place for conservation of endangered animals [26], and the audience has started to perceive these institutions as Noah's Arks. Unfortunately, many zoo studies suffer from a lack of geographic context, and zoos to the east of the former Iron Curtain have not been systematically addressed in the scientific literature to date.

Previous research has demonstrated that the number of animals and the taxonomic structure of species kept in zoos depend on many factors [11], e.g., their size, the size of their brain, and their attractiveness [27,28]. Generally, mammals have the highest preferences among visitors [26,29] and this especially applies to large charismatic ones, the so-called charismatic megafauna [28,30]. On the other hand, mammals generally have the highest requirements on space and the size of their enclosures, and as endothermic and relatively large animals, they also have high requirements on husbandry practices, including feeding and general maintenance efforts.

Quality enclosures and husbandry practices corresponding to animal needs, educational programs or conservation, and breeding activities began to be more appreciated [31]. Therefore, enclosures have been enlarged, and high-quality standards in husbandry practices were accepted according to implemented minimal standards and best-practice guidelines. This, along with the need to keep meaningfully large ex situ populations, resulted in a new trend to keep more individuals from fewer species [32]. In summary, these increased standards for maintaining sustainable ex situ populations, together with the higher specialization of modern zoos and the acceptance of the Washington Convention, could lead to a decrease in taxa kept in European zoos from the post-war period until now. This decreasing trend in the taxa richness and diversity was already predicted by Cherfas [33]. Kisling [4] and Brereton and Brereton [11] confirmed the trend of reducing the number of taxa worldwide but also the trend of growing number of zoo collections that are more similar to each other. Fraschetti and Gippoliti [34] also discussed the same declining trend for Italy, which can be inferred based on limited historical data; the number of species has sometimes declined by 50% or more in the last forty years. Mason [35] states that these trends to specialize and keep fewer species are particularly noticeable in traditional city zoos, which decrease the number of exhibits to increase their size. Colléony et al. [36] recommend more studies on how animal collections could be optimized to maximize ex situ conservation in zoos.

Taxa richness and composition in zoos represent significant components of ex situ conservation efforts. Therefore, the aim of this study was to identify the changes in taxa richness (hereinafter TR) and mammalian taxa richness (hereinafter MTR) from 1959 to 2016 in selected European zoos for which the data were available for both years. Based on the facts mentioned above and in accordance with previous findings and suggestions [4,11,33], we hypothesized that the TR and MTR will decrease between the years, and the decrease will be more prominent in mammals as they traditionally represent more demanding species to keep, especially in terms of requirements for the size of their enclosures. We further hypothesized that the decrease will be more prominent (1) for zoos established

before 1900, which used to keep large taxonomic collections while they could not expand easily in their area, and (2) for the former Western Bloc zoos, which have developed under stronger pressure from anti-zoo campaigns since the 1970s. On the other hand, zoos of the former Eastern Bloc have been popular in their countries, and moreover, they even got an opportunity to substantially improve their collections with the fall of the Iron Curtain. This is the first study investigating the development of TR and MTR in both the former Eastern and Western Blocs, regions where different post-war developments might be expected.

2. Materials and Methods

The International Zoo Yearbook (IZY), section Zoos and Aquariums of the World, was used to extract the number of taxa (corresponding to TR) and mammalian taxa (corresponding to MTR) kept in 1959 and 2016 by zoos (not including public aquaria) for which these values were available for both years. Additionally, the area size (hereinafter AS) in hectares was also extracted for all the zoos and for both years from the same source. We prefer to use the term "taxa" instead of "species" here, as it better corresponds to the fact that subspecies or animal breeds are frequently included as taxonomic units in zoo statistics. The first edition of IZY dates back to 1959; thus, this year was selected for comparison with 2016, which was the last year available in 2019, when the data extraction for this study started [37,38]. The IZY was previously used by several authors to extract data about zoo attendance [39] or about the number of species worldwide and by continents [11] and in Asia [40].

The 67 zoos for which values from 1959 and 2016 were available are located in 18 European countries. For some of the zoos (n = 7), values were not available for 1959; thus, values from 1960 [41] were used to complete the dataset. Each zoo was classified according to the time of opening: Zoos opened before 1900 (n = 26) and zoos opened during the period 1900–1960 (n = 41; factor opened with two levels); these dates were found in IZY [37] and Sheridan [12], eventually confirmed by zoo websites. Additionally, zoos were classified according to their location with respect to the former Iron Curtain: Western Bloc zoos (n = 43) and Eastern Bloc zoos (n = 24; factor region with two levels).

Statistical analyses were conducted in R, version 4.2.2, with the use of the tidyverse, ggpubr, and rstatix packages. All charts were prepared and edited in STATISTICA, version 13.5. Because the original count data were not normally distributed, descriptive statistics are given as median (MD) and median absolute deviation (MAD). Statistical tests were two-tailed, and the significance level of p-values was set at 0.05. To test whether the TR, MTR, and AS significantly changed between 1959 and 2016, we ran three separate three-way mixed ANOVAs with two between-subjects factors (opened and region) and one within-subjects factor (time; two levels, 1959 and 2016). The analysis tested the effects of these factors as well as their two-way and three-way interaction effects. Dependent variables (values of TR, MTR, and AS) were log transformed to meet assumptions, normal distribution, and homogeneity of variance for this analysis. For two dependent variables (TR and MTR), distributions of seven from a total number of eight combinations of factor levels did not depart from normality, and for one dependent variable (AS) distributions of all combinations of factor levels did not depart from normality (Shapiro–Wilk test, $p > 0.05$). As the ANOVA is quite robust against violations of the normality assumption [42], this was not an obstacle to the application of this test. Except for one combination of all factor levels for two dependent variables (MTR and AS), the data also did not include any extreme outliers. There was homogeneity of variance at each level of the within-subjects factor (time; Levene's test, $p > 0.05$), with the exception of one level for one dependent variable (AS). Interaction effects revealed by the three-way mixed ANOVAs were further investigated by post hoc tests and decomposed into simple main effects. We conducted a one-way ANOVA of one factor at each level of the second factor and used Bonferroni-adjusted p values. The difference in TR and MTR in 1959 and 2016 was also calculated for original count data, and the zoos were classified according to whether they increased or decreased the TR and MTR.

Yates' corrected $\chi 2$ test was used to compare the number of these zoos that increased and decreased their TR and MTR.

3. Results

3.1. Taxa Richness (TR)

The opening period of the zoo had a significant effect on the TR (Table 1), with zoos opened before 1900 keeping more taxa than zoos opened in the period 1900–1960, regardless of whether it was in 1959 or 2016 (Table 2, Figure 1). In 1959, TR was significantly lower for zoos of the former Eastern Bloc than for zoos of the Western Bloc ($F_{1,5} = 7.22$, p.adj < 0.05); however, there was no significant difference in 2016 ($F_{1,65} = 1.88$, p.adj = 0.35). The difference was alleviated in 2016 because the zoos of the former Western Bloc not only significantly decreased the TR ($F_{1,84} = 0.86$, p.adj = 0.72; Figure 1), but most importantly, zoos of the former Eastern Bloc significantly increased the TR ($F_{1,46} = 10.1$, p.adj < 0.05). The median number of TR kept in all observed zoos in 1959 and 2016 was essentially similar: 282 and 287 taxa, respectively.

Table 1. Effects of opening period (opened; before 1900/period 1900–1960), location with respect to the former Iron Curtain (region; Western Bloc/Eastern Bloc), and year (time; 1959/2016) tested by three-way mixed ANOVA with two between-subjects factors (opened and region) and one within-subjects factor (time). TR = taxa richness, MTR = mammalian taxa richness, AS = area size.

Effects and Their Interactions	Log TR		Log MTR		Log AS	
	F (1,63)	*p*	F (1,63)	*p*	F (1,63)	*p*
Opened	10.65	<0.05	8.71	<0.05	2.34	0.13
Region	0.01	0.91	1.4	0.24	3.33	0.07
Time	6.67	<0.05	1.13	0.29	31.59	<0.001
Opened:Region	1.38	0.25	0.21	0.65	0.2	0.66
Opened:Time	1.18	0.28	5.24	<0.05	0.87	0.35
Region:Time	20.79	<0.001	13	<0.001	6.86	<0.05
Opened:Region:Time	0.34	0.56	0.16	0.69	0.61	0.44

Table 2. Descriptive statistics, median (MD) and median absolute deviation (MAD), of taxa richness (TR), mammalian taxa richness (MTR), and area size for all zoos, including their classifications according to their opening period (opened) and location with respect to the former Iron Curtain (region). n = number of zoos.

	Time	n	Taxa Richness (TR)		Mammalian Taxa Richness (MTR)		Area Size (ha)	
			MD	MAD	MD	MAD	MD	MAD
All zoos	1959	67	282.0	228.0	83.0	50.4	15.0	7.4
	2016	67	287.0	181.0	71.0	22.2	24.0	16.3
Opened								
Before 1900	1959	26	448.0	317.0	102.0	54.1	13.8	6.2
	2016	26	440.0	386.0	68.5	20.0	17.1	9.6
Period 1900–1960	1959	41	246.0	187.0	65.0	38.5	15.4	12.4
	2016	41	263.0	187.0	71.0	22.2	28.0	17.8
Region								
Western Bloc	1959	43	188.0	131.0	64.0	36.3	14.6	6.6
	2016	43	338.0	185.0	84.0	23.7	20.0	11.9
Eastern Bloc	1959	24	372.0	243.0	88.0	48.9	15.8	11.3
	2016	24	267.0	166.0	62.0	20.8	37.2	30.1

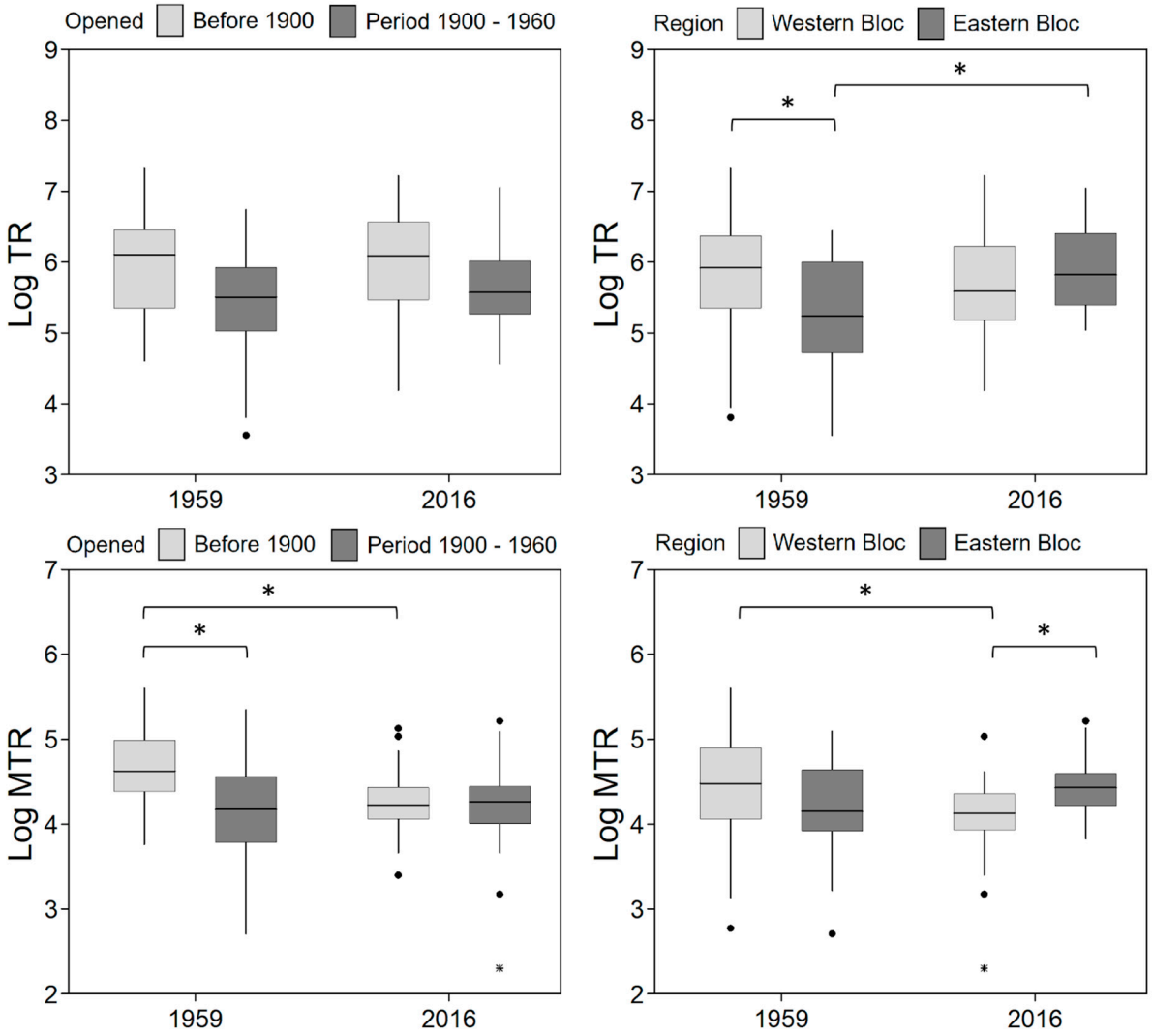

Figure 1. Differences between log-transformed taxa richness (TR) and mammalian taxa richness (MTR) in 1959 and 2016 according to the opening period (opened; left) and location with respect to the former Iron Curtain (region; right). Significant differences are marked with braces and asterisks. The boxes represent the interquartile range (IQR), the heavy line is the median, vertical lines are the lower and upper 1.5 × IQR, and circles are outliers.

Zoos that kept more taxa in 2016 than in 1959 (58.2% of the analyzed zoos) included an approximately similar number of zoos from the Western (46.2%) and Eastern Bloc (53.8%). However, Western Bloc zoos with increased taxa numbers constituted only 41.9% of all Western Bloc zoos, while Eastern Bloc zoos with increased taxa numbers constituted 87.5% of all Eastern Bloc zoos (Figure 2; $\chi 2 = 11.38$, df = 1, $p < 0.001$). In terms of the opening period, zoos opened before 1900 constituted only 30.8% of all zoos with increased taxa numbers, while zoos opened in the period 1900–1960 constituted 69.2% of these zoos. There were 46.2% of zoos opened before 1900 and 65.9% of zoos opened in the period 1900–1960 that increased their taxa numbers ($\chi 2 = 1.79$, df = 1, $p = 0.18$). Zoos with decreased taxa numbers in 2016 in comparison to 1959 (41.8% of the analyzed zoos) mostly included those of the former Western Bloc (89.3%), but equal numbers (50.0%) of the zoos opened before 1900 and in the period 1900–1960 (Figure 2).

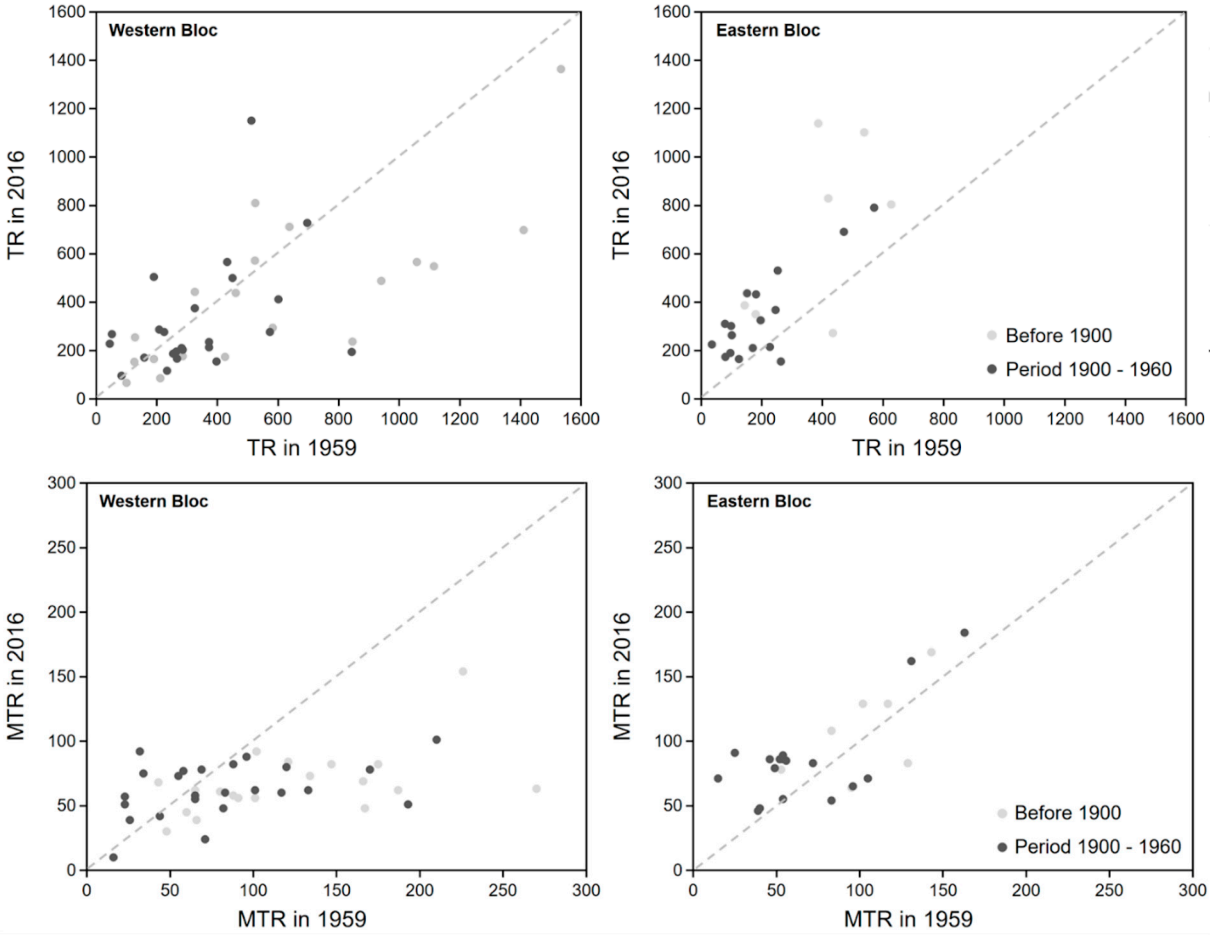

Figure 2. Taxa richness (TR) and mammalian taxa richness (MTR) of zoos from the former Western (left) and Eastern Bloc (right) in 1959 and 2016 further classified according to their opening period (before 1900/period 1900–1960). The dashed diagonal delineates the situation where the number of species would be unchanged in 2016 compared to 1959.

3.2. Mammalian Taxa Richness (MTR)

The MTR changed between 1959 and 2016, and there was a significant interaction with the opening period and the effect of the location of the zoo as included in the former Eastern or Western Bloc (Table 1). In 1959, the MTR was significantly higher for zoos opened before 1900 than for those opened in the period 1900–1960 ($F_{1,65} = 12.6$, p.adj < 0.05); however, there was no significant difference in 2016 ($F_{1,65} = 0.83$, p.adj = 0.73). While the MTR remained almost the same for zoos opened in the period 1900–1960, zoos opened before 1900 significantly decreased their MTR from 1959 to 2016 ($F_{1,50} = 9.38$, p.adj < 0.05). Although zoos of the former Eastern Bloc had a lower MTR than zoos of the Western Bloc in 1959, this difference was not significant ($F_{1,65} = 1.58$, p.adj = 0.43). However, the situation reversed in 2016, with zoos of the former Eastern Bloc having even significantly higher MTR ($F_{1,65} = 11.1$, p.adj < 0.05; Table 1). Mostly, a significant decrease in MTR for zoos of the Western Bloc contributed to this reversed situation ($F_{1,84} = 6.69$, p.adj < 0.05).

Zoos that kept more mammalian taxa in 2016 than in 1959 (41.8% of the analyzed zoos) included a higher number of Eastern Bloc zoos (67.9%) than Western Bloc zoos (32.1%). The number of mammalian taxa was increased by 79.2% of all analyzed Eastern Bloc zoos, but the same applies to only 20.9% of all Western Bloc zoos ($\chi 2 = 19.15$, df = 1, $p < 0.001$). In terms of the opening period, zoos opened before 1900 constituted only 21.4% of all zoos with increased taxa numbers, while zoos opened in the period 1900–1960 constituted 78.6% of these zoos. There were 23.1% of zoos opened before 1900 and 53.7% of zoos opened in the period 1900–1960 that increased their mammalian taxa numbers ($\chi 2 = 4.94$, df = 1,

$p < 0.03$). Zoos with decreased mammalian taxa numbers in 2016 in comparison to 1959 (58.2% of the analyzed zoos) mostly included those of the former Western Bloc (87.2%) and a similar number of zoos opened before 1900 and in the period 1900–1960, 51.3% and 48.7%, respectively (Figure 2).

3.3. Area Size (AS)

There was no significant change in AS with respect to the opening period (Table 1); however, zoos of the former Eastern Bloc significantly increased their AS between 1959 and 2016 (F1.46 = 8.07, p.adj < 0.01). Thus, although there was no significant difference in AS between zoos of the former Western and Eastern Bloc in 1959, AS of the zoos of the former Eastern Bloc was significantly larger in 2016 (F1.65 = 10.6, p.adj < 0.05).

4. Discussion

All zoos have a limited capacity [43], and with a growing emphasis on animal welfare [44], enlarged exhibit size, and growing requirements for increased ex situ population size, this capacity will even decrease. Under such circumstances, zoos must carefully consider which species/taxa to remain to function as a "Noah's Arks'" ex situ population of endangered taxa, but also to be sufficiently attractive to visitors [45]. Previous authors predicted or even demonstrated the declining trend in the number of taxa kept. Brereton and Brereton [11] showed that the average TR and MTR in zoos worldwide has decreased rapidly from 329 to 225 taxa and from 81 to 43 mammal taxa between 1960 and 2018.

Our study examines the changes in median TR and MTR in European zoos during almost the same period, from 1959 to 2016, and includes only those institutions for which the data for both years were available. This resulted in a smaller sample size of 67 institutions but allowed us to investigate the changes within the same list of zoos. The present study also considers the potential effects of their opening period and location with respect to the former Iron Curtain, which in principle meant a different development on both sides. Our results did not support the hypothesis that median TR and MTR in European zoos is decreasing in general; however, they showed that the developmental trends are rather dependent on the location of zoos with respect to the former Iron Curtain. Moreover, the development of the median MTR is also dependent on the opening period.

The present study did not find any significant decrease in median TR between the analyzed years; however, it found a significant decrease in median MTR for zoos opened prior to 1900 as well as zoos of the former Western Bloc. This partially supported our hypothesis that the decreasing trend will be stronger for mammals, which generally have high requirements on the size of their enclosures and husbandry practices. On the other hand, zoos opened in the period 1900–1960, and those of the Eastern Bloc showed the opposite, albeit a non-significant trend. Mammals play an essential role in the taxa composition of zoos [46]; the ratio between the number of species kept in zoos and the number of species known worldwide is the best in the case of mammals [47]. Charismatic megafauna, usually represented by mammals, constitute "crowd pullers" [33], which typically attract the public [48,49] and play a key socio-economic role as these animals influence attendance in a positive way [50]. Without such biocapital animals, zoos would close because of financial difficulties [51]; the effect of the number of mammals on visitor attendance overcomes the effect of the number of all taxa kept [52]. Moreover, charismatic megafauna can also be designated as ambassadors for biodiversity conservation [53]. Conservation strategies based on charismatic flagship species are successful among donors [54]. Mammals are the most often crowdfunded animals worldwide [55], and as "flagship species", they can draw more visitors to support in situ conservation, thus helping to fulfill one of the goals of modern zoos [46,52,54,56]. Additionally, most conservation programs in the 20th century were concerned with large mammals [57], and nearly half of all studbooks are kept for mammals [58], which are other important attributes motivating zoos to keep them.

The zoos opened before 1900 significantly decreased the MTR between 1959 and 2016, which also partially (the same trend was not found for TR) supported our hypothesis that

the decrease will be more prominent in such institutions. These zoos were traditionally set up and maintained as taxonomically rich collections, which, however, have noticeably reduced the number of taxa kept. This can be illustrated by the world's most taxa-rich zoo, the Berlin Zoo, which kept 504 mammal taxa in 1883 [59], 226 in 1959, and "only" 154 mammal taxa in 2016. Additionally, the early period of establishment of these zoos largely determined their location and size; they were usually up to 20 ha in size and located on the outskirts of cities, which completely absorbed them within the course of their further development [13]. Consequently, these zoos, still belonging to today's leading European zoos, have only limited possibilities for growing in size. These zoos also include buildings, which are protected as heritage monuments, and the possibilities of changes are also restricted [60]. At the same time, they have gone through considerable structural changes, both to improve animal husbandry and to maintain visitors' experiences.

Consistent with our hypothesis, zoos of the Western Bloc significantly decreased the median MTR and only marginally decreased the median TR between 1959 and 2016. Surprisingly, Eastern Bloc zoos showed an opposite trend in median TR and MTR, with the former also identified as a significant increase. Within the former Eastern Bloc zoos, there are only a few zoos established before 1900. Compared to the "traditional" Western Bloc zoos, most Eastern Bloc "traditional" zoos started to develop after the Second World War [15] and were relatively new in 1959. Consequently, in some cases, they did not have many animals to exhibit at that time. Moreover, many of them were founded outside urban centers; thus, they often can still grow and are not limited by space to such a large extent. Results of the present study confirm that median AS significantly increased for zoos of the former Eastern Bloc between 1959 and 2016. Finally, opening state borders after the fall of the Iron Curtain around 1990 enabled broader international cooperation and further dramatic transformation. Many new exotic species that partially replaced or complemented relatively commonly kept species have been imported and many of the former Eastern Bloc zoos seized the opportunity to establish extensive collections. For example, nowadays, these zoos contain the largest amphibian collections in Europe [61].

The fact that we did not find an obviously decreasing trend in median TR for selected European zoos may be attributed to several reasons. First, when working with the same set of zoos, the decreasing trend might be mitigated by not including new, thus a priori less species-rich zoos, at the end of the observed period. Second, the decreasing trend might also be mitigated by substantial taxonomical changes that have been launched since the introduction of molecular genetic methods. The number of scientifically identified species has increased, although mainly due to taxonomic inflation [62], based on a shift in paradigm from the biological species concept to the phylogenetic species concept [63]. However, it is not known to what extent this phenomenon eventually biases the results of studies focused on developmental trends in the number of taxa kept in zoos.

Finally, the most effective strategy to combat limited space is a shift from a part of the large charismatic mammals towards smaller species, particularly amphibians, invertebrates, and fishes [11,16,47,52]. Among others, one of the current trends is establishing—among visitors, very popular—aquariums as a part of zoological gardens [6,16]. Additionally, although the majority of iconic animals are still the same as in the 19th century (e.g., elephants or big cats) [64], smaller, cute species that do not need such large and expensive enclosures can be attractive, typically social and active species such as otters [65], and have also become iconic. Meerkats and ring-tailed lemurs [12] are probably the most famous examples. At the same time, ca. 53% of zoo populations of all species worldwide have fewer than 50 individuals, making the maintenance of genetically and demographically stable populations in the long term extremely challenging [66].

5. Conclusions

Zoos increasingly perceive their role in the field of nature conservation and react, among other things, by changing the taxa numbers and composition. Examining and understanding these changes, i.e., which taxa are kept in what numbers and what is their

role in fulfilling the established zoo and aquaria conservation missions, should be pivotal for appropriate future planning of zoo collections. This raises an important message about the relevance of zoos as ex situ conservation institutions. Zoos across Europe are at different stages of development and, based on this, have different conditions for further (conservation) development. Additionally, European zoos are currently facing new political, cultural, and socio-economic threats (e.g., Brexit, COVID-19 pandemic, war in Ukraine, anti-zoo campaigns), which may have different effects in different regions of Europe. In this context, the results of the present study point to an important fact that European zoos (and therefore zoos worldwide) have not been subject to developmental trends uniformly. Thus, to fulfill conservation priorities and current requirements for animal husbandry and welfare, while concurrently making appropriate use of their specific potential, zoos should apply appropriate strategies based on their regional and historical development when facing future challenges. This study is an initial contribution to the topic, where more detailed analyses of the development trends of zoos and their ex situ conservation mission are needed.

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